Science of the Total Environment 664 (2019) 203–214

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Modeling the present and future distribution of arbovirus vectors *Aedes aegypti* and *Aedes albopictus* under climate change scenarios in Mainland China

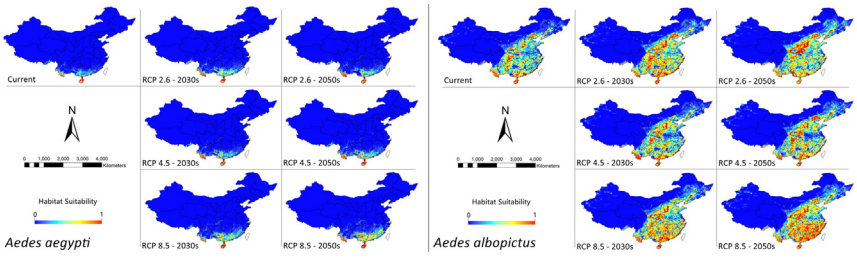
Boyang Liu [a,b], Xiang Gao [a,b], Jun Ma [a,b], Zhihui Jiao [a,b], Jianhua Xiao [a,b], Muhammad Abid Hayat [a], Hongbin Wang [a,b,*]

[a] Department of Veterinary Surgery, College of Veterinary Medicine, Northeast Agricultural University, Harbin, Heilongjiang Province, People's Republic of China
[b] Key Laboratory of the Provincial Education Department of Heilongjiang for Common Animal Disease Prevention and Treatment, College of Veterinary Medicine, Northeast Agricultural University, Harbin, Heilongjiang Province, People's Republic of China

HIGHLIGHTS

- *Aedes aegypti* and *Aedes albopictus* are vectors of various arbovirus diseases, represented mainly by dengue fever.
- Future climate changes may drive the habitat shift of mosquitoes.
- Ecological niche modeling method was used to model the current and future distribution of mosquitoes.
- Both species were predicted to expand their habitat under future climate assumptions.
- Temperature, precipitation and cropland show significant impact on the survival of mosquitoes.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 23 November 2018
Received in revised form 17 January 2019
Accepted 23 January 2019
Available online 1 February 2019

Editor: Scott Sheridan

Keywords:
Aedes aegypti
Aedes albopictus
Future climate change
Ecological niche model
Vector-borne diseases

ABSTRACT

Aedes aegypti and *Aedes albopictus* are two important mosquito species which transmit various infectious arbovirus diseases represented mainly by dengue fever. These two species of mosquito have a wide range of distribution and strong transfer capacity. With ongoing global climate change, we are facing an increasing public health threat from the rapid spread of vectors in wider geographical areas. Based on observed occurrence records of *Ae. aegypti* and *Ae. albopictus* and high-resolution environmental layers reflecting climate and land-use conditions, a Maxent niche modeling approach was adopted to model the current and future distribution of both species in Mainland China. Our models provide predictions of suitable habitat shifts under future climate scenarios up to the 2050s. Both species were predicted to expand their niche range to varying degrees under future climate scenarios. *Aedes aegypti* was modeled to expand its habitat from Guangdong, Guangxi, Yunnan and Hainan to Fujian, Jiangxi and Guizhou. *Aedes albopictus* was modeled to increase magnitude of distribution within its present range of northern, southwestern and southeastern coastal areas of Mainland China. Area and population exposed to mosquitoes are predicted to increase significantly. Environmental variables that have significant impact on the distribution of mosquitoes are also revealed by our model. The results of our study can be referenced in further ecological studies and will guide the development of strategies for the prevention and control of mosquito-borne diseases.

© 2019 Elsevier B.V. All rights reserved.

* Corresponding author at: Department of Veterinary Surgery, College of Veterinary Medicine, Northeast Agricultural University, Harbin 150030, Heilongjiang Province, People's Republic of China.
E-mail address: hbwang1940@163.com (H. Wang).

https://doi.org/10.1016/j.scitotenv.2019.01.301
0048-9697/© 2019 Elsevier B.V. All rights reserved.

1. Introduction

Vector-borne diseases are a common global health threat due to the worldwide distribution of different vectors. Mosquitoes are commonly vectors that can transmit a variety of infectious diseases, both animal and human. Dengue fever (DF) is an acute infectious disease, and is one of the most important arbovirus diseases. It is estimated that there are 390 million global infections of DF per year (Bhatt et al., 2013). More than 125 countries are affected by dengue virus all over the world (Ferreira, 2012). The spread of dengue is thought to be caused predominantly by international trade and travel, urbanization, insufficient vector monitoring and global climate change (Hales et al., 2002; Morrison et al., 2008; Gubler, 2012; Murray et al., 2013). The first documented outbreak of DF in Mainland China was in Foshan, Guangdong province in 1978 (Zhang et al., 2014). Since then, the epidemic of DF mainly occurred in the southern provinces of Mainland China, such as Guangdong, Guangxi, Hainan and Fujian (Wu et al., 2010). However, in recent years, the geographic distribution of DF has expanded to include the northern and inland regions of China. In 2004, DF cases were confirmed in Zhejiang province (Xu et al., 2007). In 2008, the first outbreak of DF caused by local infection was reported in Yunnan province (Li et al., 2010). In 2013, the first outbreak of DF in central China was reported in Henan province (Yong et al., 2014).

Dengue virus is transmitted primarily by *Aedes aegypti* and *Aedes albopictus*. *Ae. aegypti* is the primary vector in the transmission of dengue and *Ae. albopictus* acts as the secondary vector (Kong et al., 2018). *Ae. aegypti* originated in Africa but is currently distributed in tropical and sub-tropical regions of the world (Brown et al., 2014). *Ae. albopictus* is one of the most rapidly spreading invasive species in the world (Boes et al., 2014). The original habitat of *Ae. albopictus* is in East Asia, but has been observed to be rapidly invading other continents (Benedict et al., 2007). In addition to dengue fever, *Ae. aegypti* and *Ae. albopictus* are also competent vectors of many other arbovirus diseases, such as chikungunya fever, yellow fever, Rift Valley fever and West Nile fever (Moutailler et al., 2008; Jentes et al., 2011; Leparc-Goffart et al., 2014; Joubert and O'Neill, 2017). Therefore, we are facing an increasing public health threat of arbovirus diseases due to the spread of mosquitoes.

There is a major concern that no available vaccine or specific antiviral therapy exists to prevent or treat dengue (Wildersmith et al., 2010). Currently, the only effective approach to prevent and control dengue is to control mosquitoes populations. Ecological niche modeling is a widely accepted approach to predict the potential distribution of various species, microorganisms and even epidemic diseases (Chikerema et al., 2013; Wang et al., 2014; Arnould et al., 2015; Gao et al., 2016; Manyangadze et al., 2016). Based on records in which occurrence is documented, alongside environmental variables considered to have an impact on the target species, the relationship between them can be estimated by using statistical algorithms. Risk assessments of vector-borne diseases by modeling the distribution of vectors have been highlighted in many previous studies, such as the modeling of *Culex tritaeniorhynchus* for Japanese encephalitis, *Phlebotomus chinensis* for Leishmaniasis, and *Culex pipiens* for West Nile virus and Rift Valley fever (Miller et al., 2012; Conley et al., 2014; Gao et al., 2018). Species distribution models can help improve the targeted monitoring of vectors and guide the implementation of controlling programs (Ren et al., 2016; Sallam et al., 2016).

Based on the increasingly serious situation for prevention and control of mosquito-borne diseases in Mainland China, it is essential to better understand the distribution of mosquito vectors. Due to the lack of a comprehensive national program for mosquito surveillance, little is known about the distribution of mosquitoes. We therefore adopted the niche modeling method to assess the current distribution of *Aedes* mosquitoes for Mainland China, based on existing presence records. In addition, our modeling took into account the possibility of mosquito habitat expansion caused by climate change. This enabled predictions to be made for future habitats for the decades 2030s and 2050s. We used the assumptions of future climate conditions to account for the uncertainty of global climate change.

2. Methods

2.1. Mosquito occurrence data

The larvae and adult collections of *Ae. aegypti* and *Ae. albopictus* in Mainland China were obtained from two sources. Firstly, a comprehensive and systematic literature retrieval was performed. Articles which provided detailed information on collection locations to confirm coordinates were adopted, and only records from 1990 to date were included. From these articles, 42 unique records of *Ae. aegypti* and 144 unique records of *Ae. albopictus* were obtained. The second source was the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org/), which contains global occurrence records of a large number of species. No *Ae. aegypti* records were retrieved, but 38 unique records of *Ae. albopictus* were obtained from this source. Since our study was performed under the resolution of 2.5 arcmin (approximately 5 km × 5 km), records within one grid cell were considered as one point. Finally, 42 points of *Ae. aegypti* and 177 points of *Ae. albopictus* were included in the final mosquito database (S1 Table).

2.2. Environmental variables and data processing

Nineteen bioclimate variables and twelve land-use variables were used to establish the model (Table 1). Data for current climate conditions were accessed and downloaded from WorldClim (http://worldclim.org/version1). Variables in this dataset, representing temperature and precipitation conditions, were provided as the baseline for future scenarios. Data for future climate conditions were provided by the Consultative Group for International Agricultural Research (CGIAR) Research Program on Climate Change, Agriculture and Food Security (CCAFS) (http://ccafs-climate.org/). The assumptions for future climate conditions were derived from the fifth IPCC assessment report (AR5). The IPCC coordinates climate research communities to develop a set of scenarios which reflect possible climate conditions for the twenty-first century. The "Representative Concentration Pathways" (RCPs) describes assumptions about the possible future emission of greenhouse gases (Vuuren et al., 2011). RCPs under the Climate System Model of the Beijing Climate Center (BCC-CSM1-1) model were used in our study. The BCC-CSM1-1 climate model is one of the most commonly used models for simulating the climate change in China (Zhang et al., 2018). We chose RCP 2.6 as the minimum emission scenario, RCP 4.5 as the medium, and RCP 8.5 as the maximum. Both current and future variables have a high resolution of 2.5 arcmin (approx. 5 km × 5 km).

Land-use variables were downloaded from the Land-Use Harmonization (LUH2) database (http://luh.umd.edu/index.shtml). A dataset of land-use scenarios at 0.25° × 0.25° resolution from 850 to 2100 were provided as part of the World Climate Research Program Coupled Model Intercomparison Project (CMIP6).

We extracted future bioclimate and land-use variables with the same RCPs (RCP 2.6, RCP 4.5 and RCP 8.5) and time periods (2030s and 2050s). All environmental layers were resampled to 2.5 arcmin (approx. 5 km × 5 km) resolution using bilinear interpolation and cropped to the geographical area of Mainland China. All operations were accomplished in ArcGIS 10.2 (ESRI Inc., Redlands, CA, USA).

Multicollinearity test of these variables was performed by calculating the variance inflation factor (VIF), using the *car* package in R (Arnould et al., 2015; Olivero et al., 2016; Pradhan, 2016). Variables with VIF > 10 were considered to have collinearity problem (Kubota et al., 2015). Finally, variables with significant collinearity were removed from the model (Table 1).

Table 1
Variables used in the model.

Bioclimate	Description	Included	Land-use	Description	Included
Bio1	Annual mean temperature		Primf	Forested primary land	Yes
Bio2	Mean diurnal range	Yes	Primn	Non-forested primary land	Yes
Bio3	Isothermality		Secdf	Potentially forested secondary land	Yes
Bio4	Temperature seasonality	Yes	Secdn	Potentially non-forested secondary land	Yes
Bio5	Maximum temperature of the warmest month	Yes	Pastr	Managed pasture	
Bio6	Minimum temperature of the coldest month		Range	Rangeland	Yes
Bio7	Temperature annual range		Urban	Urban land	Yes
Bio8	Mean temperature of the wettest quarter		C3ann	C3 annual crops	Yes
Bio9	Mean temperature of the driest quarter		C3per	C3 perennial crops	Yes
Bio10	Mean temperature of the warmest quarter		C3nfx	C3 nitrogen-fixing crops	Yes
Bio11	Mean temperature of the coldest quarter		C4ann	C4 annual crops	Yes
Bio12	Annual precipitation		C4per	C4 perennial crops	Yes
Bio13	Precipitation of the wettest month				
Bio14	Precipitation of the driest month	Yes			
Bio15	Precipitation seasonality	Yes			
Bio16	Precipitation of the wettest quarter				
Bio17	Precipitation of the driest quarter				
Bio18	Precipitation of the warmest quarter	Yes			
Bio19	Precipitation of the coldest quarter				

2.3. Establishing the Maxent models

Maxent 3.4.1 (http://biodiversityinformatics.amnh.org/open_source/maxent/) is one of the most widely used niche modeling methods and was used to establish the model (Dan and Seifert, 2011). Among various presence-only modeling methods, Maxent has shown outstanding predictive performance in modeling the niches of species, and scores well in comparative studies (Elith et al., 2006; Wisz et al., 2008; Phillips and Dudík, 2010). Maxent has also been demonstrated to provide more useful models than other methods in the case of small sample sizes, although more presence records (>30) are recommended (Baldwin, 2009). We set 25% of the occurrence points as test points (randomly selected by the program), and the remaining 75% as training points (Phillips, 2017). The average of 100 replicates for each model were taken as the final predictions (Conley et al., 2014).

Sampling bias is a common problem in species distribution modeling (Kramer-Schadt et al., 2013). Sampling locations are usually biased toward areas which are conveniently accessed. This may result in the observed species distribution not reflecting the real distribution. To counter the sampling bias, "pseudo-absences" with the same spatial bias as the presence points are recommended to introduced into the model (Phillips et al., 2009; Brown, 2017). To this end, SDMtoolbox v2.2 (http://sdmtoolbox.org/), a python-based tool for ArcGIS, was used to generate 10,000 background points with the same bias (Elith et al., 2010).

2.4. Estimating the exposed area and population

Binary models are widely used to convert suitability for species into presence/absence in species distribution modeling. To estimate the area that is suitable for mosquito survival, sensitivity equals specificity threshold based on the mean value of 100 replicates was applied to generate binary models (Liu et al., 2010; Liu and Newell, 2013; Conley et al., 2014; Cunze et al., 2016). A 2010 global population density grid with 2.5 arcmin (approx. 5 km × 5 km) resolution was used to estimate the current and future population exposed to mosquitoes (http://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density-rev10). Future population density grids were created by multiplying the value of urban pixels by the urban population growth rate, and rural pixels were multiplied by the rural population growth rate, which obtained from Population Estimates and Projections, World Bank Group (https://datacatalog.worldbank.org/dataset/population-estimates-and-projections). The DMSP-OLS nighttime light data was widely used to identify the extent of urban (https://ngdc.noaa.gov/eog/dmsp/downloadV4composites.html) (Sutton, 2003; Small et al., 2005). The pixel value of each grid cell represents the annual average brightness of nighttime light. In China, grid cells with pixel value >12 were commonly considered as urban areas (Ma et al., 2012; Fan et al., 2014).

2.5. Model evaluation and interpretation

The receiver operating characteristic curve (ROC) was used to evaluate the model performance. A greater area under the curve (AUC) value (0–1) indicates a better predictive performance. The partial receiver operator characteristics (pROC) was chosen as an additional measure to provide a firmer foundation for the evaluation of model performance, because of the shortcoming of equally weighting omission and commission errors of traditional ROC approach (Peterson et al., 2008). We calculated AUC ratios of pROC at the error tolerance (E) of 5% and test statistical significance with Z test (Chetan et al., 2014; Escobar et al., 2018).

In addition to the AUC given by modeling with all variables, Maxent also gives the AUCs when modeling with each variable individually. "Response curves" generated by Maxent reflect the dependence of predicted suitability on each variable.

3. Results

3.1. Current distribution of Aedes aegypti and Aedes albopictus

The modeling results are shown in Figs. 1 and 2. Both models performed well in representing the distribution of occurrence records. Both models were statistically significantly better than null expectations, with the mean AUC ratio of 1.980 for *Ae. aegypti* and 1.695 for *Ae. albopictus* ($P < 0.01$).

Ae. aegypti has a limited ecological niche in southern Mainland China. Suitable habitats for *Ae. aegypti* are distributed in most of Hainan, southern Guangdong and Guangxi, and southwestern Yunnan. *Ae. albopictus* is more extensively distributed, distributed in southern, eastern and central regions, and even in parts of the northeastern China. These two species have different ecological niches, while they also share common habitats in southern China. Most of Hainan, southern Guangdong, southeastern Guangxi and southwestern Yunnan are considered suitable habitats for both species.

3.2. One-variable models

Seventeen one-variable models were created for two species by Maxent, respectively (all AUCs are shown in S2 Table). Models with AUC > 0.8 for both species were chosen to illustrate response curves

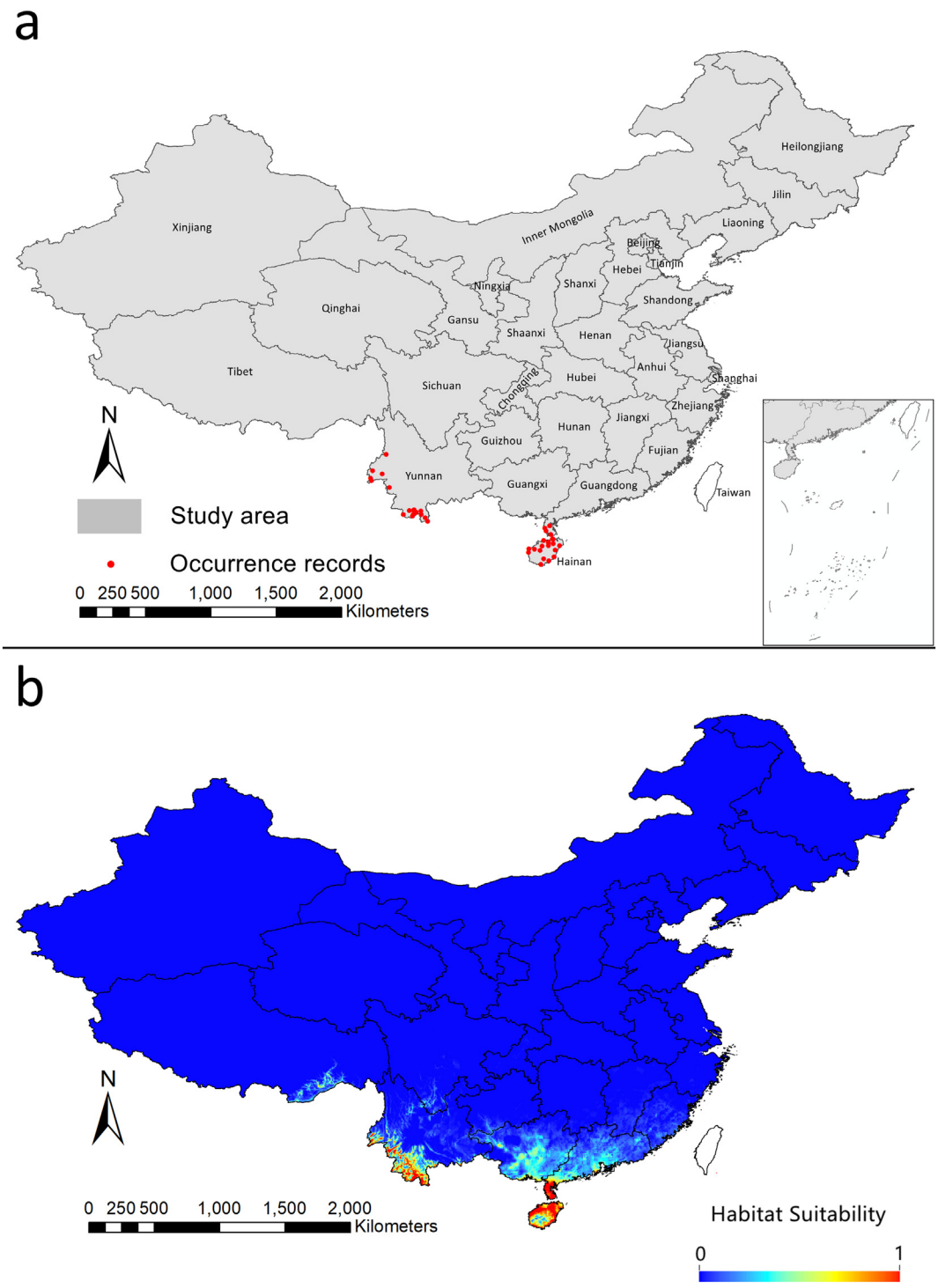


Fig. 1. Observed and modeled distribution of *Aedes aegypti* in Mainland China. a. Occurrence records of *Ae. aegypti*. b. Modeled habitat suitability of *Ae. aegypti* under current climate and land-use conditions.

(Fig. 3). These variables are considered to have significant effect on the survival of both species. Negative effects to mosquito habitat suitability were observed as the increasing of mean diurnal range (Bio 2) and seasonality (Bio 4) of temperature. There is predicted to be a peak of habitat suitability and then decline as the increasing of precipitation in the driest month (Bio 14). Precipitation of the warmest quarter (Bio 18) shows positive effect to the survival of mosquitoes. The effect of the increasing of croplands (C3nfx and C4per) on the habitat suitability is generally rise first and then drop (C3nfx on both species and C4per on *Ae. albopictus*) or then stable (C4per on *Ae. aegypti*).

3.3. Distribution prediction under future climate scenarios

Suitable habitat transfer and expansion was predicted to occur for both species under future climate scenarios (Figs. 4 and 5). *Ae. aegypti* still inhabit southern Mainland China and there is also predicted to be a significant expansion. Under the RCP 2.6 and 4.5 scenarios, *Ae. aegypti*

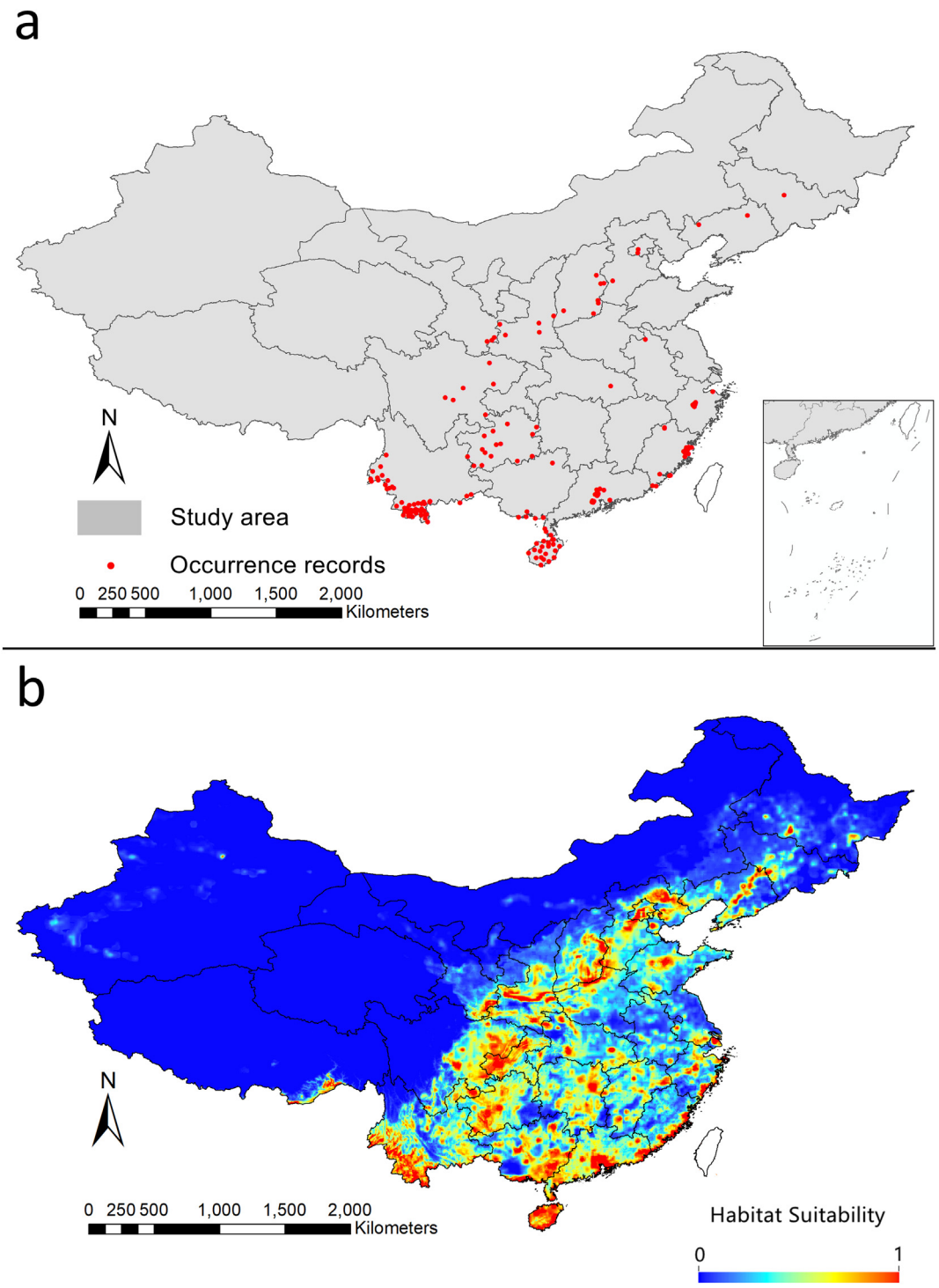


Fig. 2. Observed and modeled distribution of *Aedes albopictus* in Mainland China. a. Occurrence records of *Ae. albopictus*. b. Modeled habitat suitability of *Ae. albopictus* under current climate and land-use conditions.

will expand its habitat in most of Guangdong and Guangxi, and southern Guizhou. Under the RCP 8.5 scenario, nearly the whole of Guangdong and Guangxi will be suitable for the survival of *Ae. aegypti*. Most of Fujian and southern Jiangxi, which are currently unsuitable areas, have a high probability of becoming future habitats for *Ae. aegypti*. There is also a possibility that *Ae. aegypti* will invade Sichuan and Chongqing. *Ae. albopictus* was predicted to expand its habitat under all scenarios. However, the expansion is hardly reflected on its western and northern boundary, but mainly within its current range. Under RCP 2.6, expansion may occur in Hunan, Guangxi and Guangdong in the 2030s and Shanxi, Shaanxi and Henan in the 2050s. Under the RCP 4.5, expansion is predicted to mainly occur in central and northern areas. The most dramatic and serious expansion will occur under RCP 8.5, for which it is predicted that most of southern China will become suitable habitats for *Ae. albopictus*. According to the binary models, both species are predicted to expand their habitats in the future, and there will also be an expansion of areas that are common habitats for both species (Fig. 6).

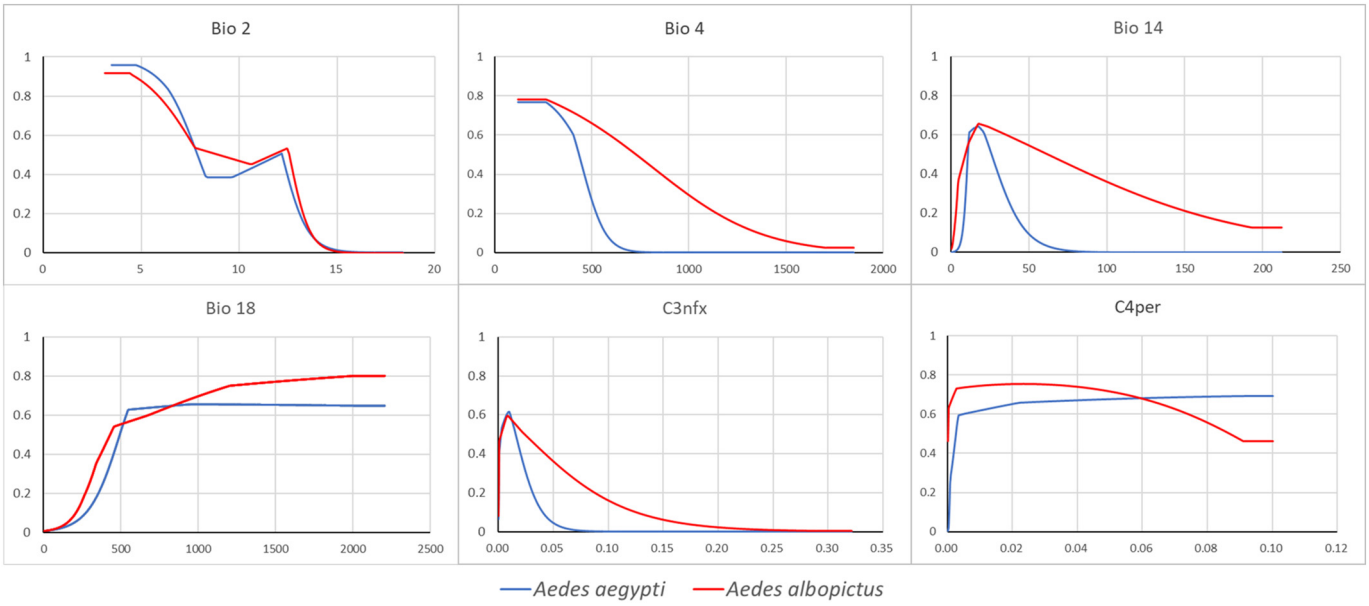


Fig. 3. Response curves for representative variables. The vertical axis represents the habitat suitability of mosquitoes, and the horizontal axis represents the variation range of the corresponding variable.

3.4. Estimates of exposed area and population

Exposed area and population were calculated based on binary models. The current habitat area of *Ae. aegypti* is estimated to be 169,849 km^2, and 894,416 km^2 for *Ae. albopictus*. Most of the area currently exposed to *Ae. aegypti* and *Ae. albopictus* are predicted to remain stable in future scenarios (Fig. 7). However, suitable area for both species will increase continuously until the 2050s under all scenarios except *Ae. aegypti* under RCP 2.6. The habitat estimation under RCP 8.5 is predicted to gain the largest area.

The number of people exposed to *Ae. aegypti* will be the largest under RCP 8.5 in both the 2030s and 2050s (Fig. 8). In the 2030s, the exposed population under RCP 4.5 is the smallest and in the 2050s the smallest exposed population occurs under RCP 2.6. The exposed population for *Ae. aegypti* is estimated to rise continuously until the 2050s under both RCP 4.5 and 8.5. However, from the 2030s to the 2050s, it is estimated to decline under RCP 2.6. For Ae. *albopictus*, the exposed population under RCP 2.6 is the largest in the 2030s and the largest exposed population occurs under RCP 8.5 in the 2050s. The scenario of RCP 4.5 results in the smallest exposed population. The exposed population continues to rise under all three scenarios.

4. Discussion

The monitoring of arbovirus vector, such as mosquitoes, is of great significance for the prevention and control of vector-borne infectious

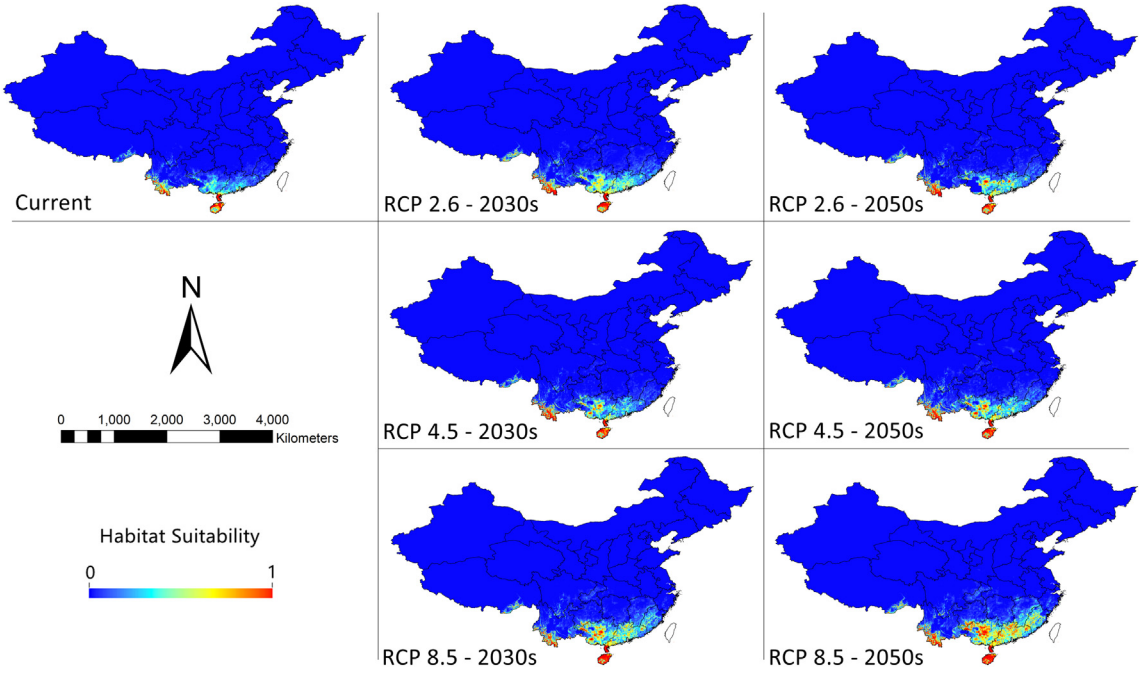


Fig. 4. Predicted habitat suitability of *Aedes aegypti* under current and future climate change scenarios.

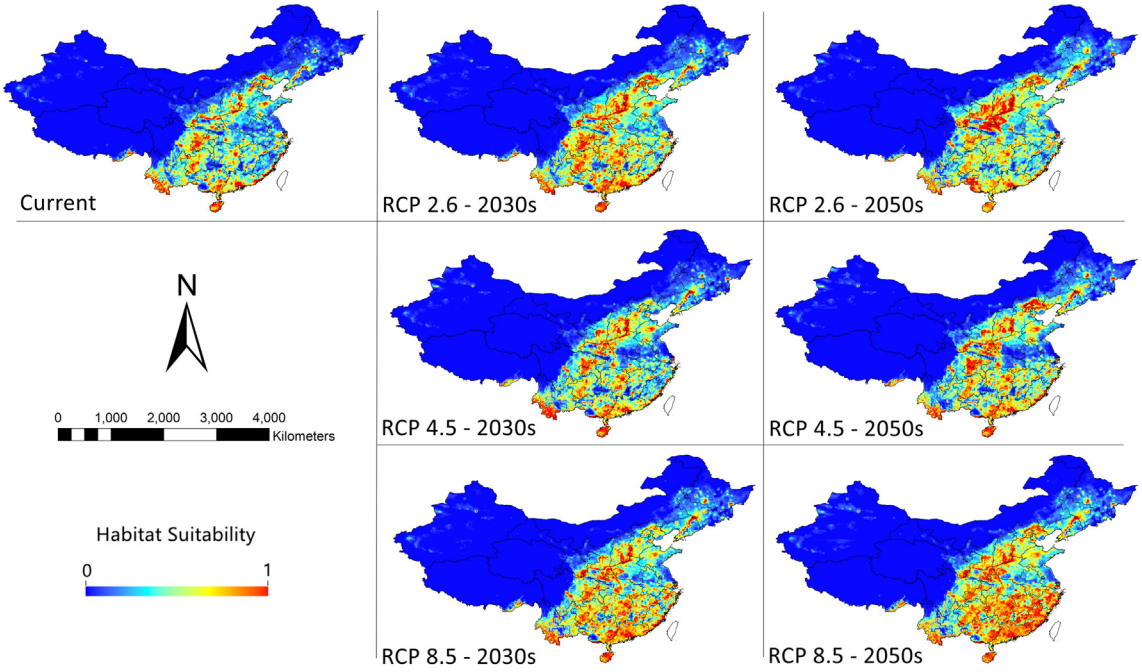


Fig. 5. Predicted habitat suitability of *Aedes albopictus* under current and future climate change scenarios.

diseases. Since the first occurrence of DF in China, both the surveillance and eradication programs for *Aedes* mosquitoes have been carried out for many years. However, its habit of being adept escaping detection in inaccessible areas makes it difficult to be targeted. The vector eradication efforts and dengue prevention in other countries, such as Singapore, which are representative, are still struggling (Ooi et al., 2006). The vast territory of China makes the situation even more severe. Targeted and purposeful monitoring and verification can be carried out according to the habitat suitability map to guide the pathogen detection of *Aedes* mosquitoes. It can also reduce the consumption and improve efficiency of the eradication work.

Although the eradication of *Ae. aegypti* in Guangxi was announced at the end of the last century and no *Ae. aegypti* was found in the 2002 survey, there are no recent reports to indicate whether it has re-established its habitat in this region (Jianren, 1991; Tan et al., 2004). In the current model, the central and southern parts of Guangxi are predicted to be suitable habitats. This shows that Guangxi still has the environmental conditions suitable to promote the survival of *Ae. aegypti* and indicates that it is still necessary for continuous vector monitoring in Guangxi. In the future models, we observed a significant expansion in the distribution of *Ae. aegypti* in Guangxi and Guangdong. The future habitat in Guangxi is predicted to extend northward to the south of Guizhou. In

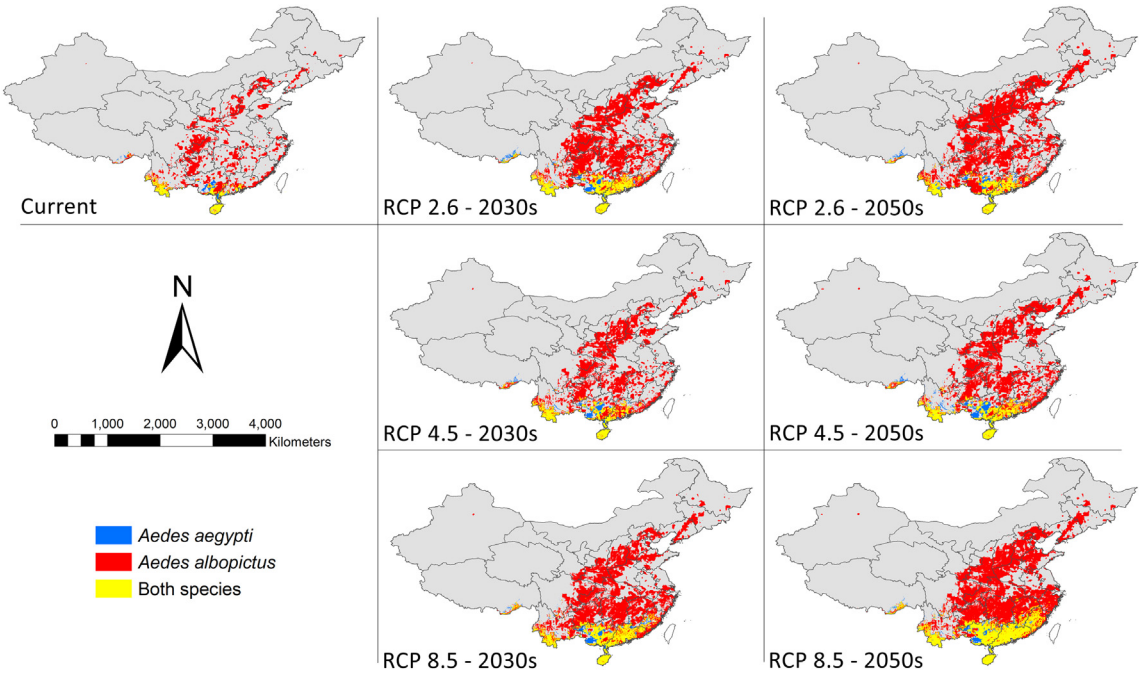


Fig. 6. Modeled suitable habitat for *Aedes aegypti* and *Aedes albopictus* under current and future climate change scenarios. The threshold of sensitivity equals specificity was applied to generate binary models.

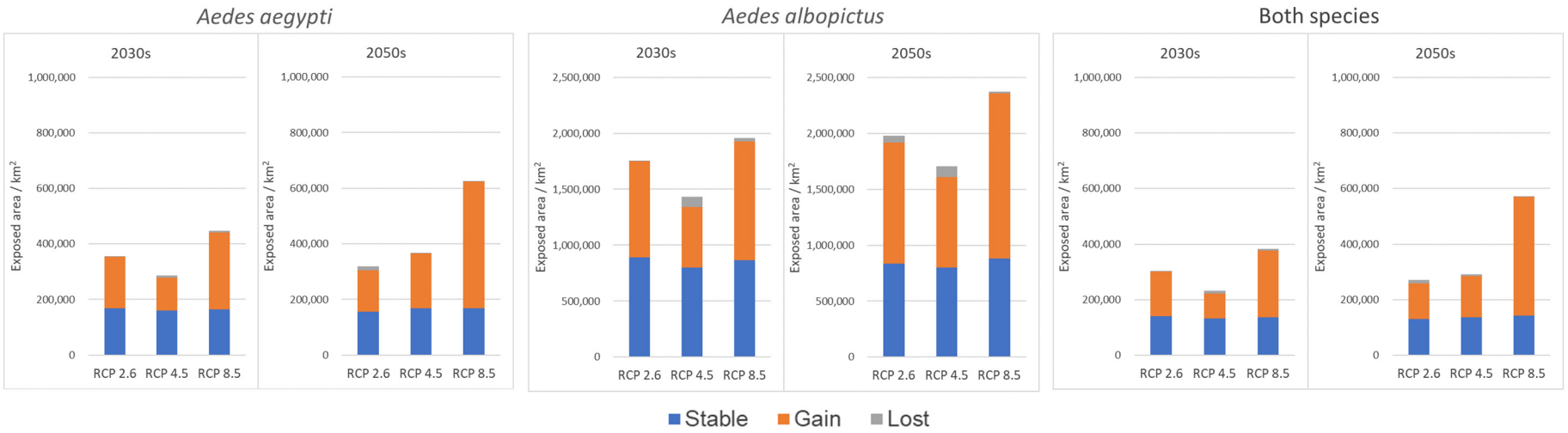


Fig. 7. Estimated gain, stable and lost of exposed area for both species under future climate change scenarios.

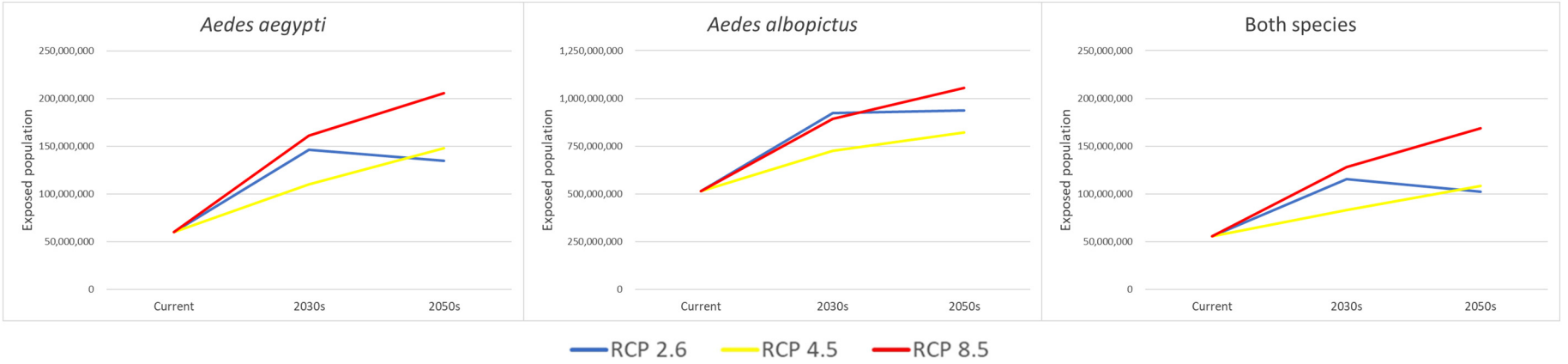


Fig. 8. Estimated change of exposed population for both species under future climate change scenarios.

Guangdong, it is predicted to extend eastward to Fujian, and most of Fujian could become habitat for *Ae. aegypti* until the 2050s under the RCP 8.5 scenario.

Ae. albopictus is currently more widely distributed in Mainland China, and is predicted to expand further in the future. It is predicted that in northern China, Shaanxi, Shanxi, Hebei, northwestern Henan and Shandong will become more suitable for the survival of *Ae. albopictus*. Even the habitats in northeast China are predicted to expand to some extent. Extensive areas in southern China will become suitable habitats for *Ae. albopictus*, such as Guizhou, Hubei, Hunan, Jiangxi, Zhejiang, Guangxi, Guangdong and Fujian. However, southeastern Henan, northern Anhui, and most of Jiangsu will remain unsuitable for the survival of *Ae. albopictus* under all scenarios. Common habitats shared by both species are mainly distributed in areas of Guangxi, Guangdong, Hainan and southwestern Yunnan and these habitats are predicted to remain stable until the 2050s. Therefore, vector surveillance in these areas needs to be strictly maintained.

The response curves to assess the effects of different variables, reflect the different environmental requirements of the two species. According to Bio 2 (Mean diurnal range) and Bio 4 (Temperature seasonality), these two species of mosquito show different dependence on temperature conditions. *Ae. albopictus* shows a greater adaptability to day-night and seasonal temperature differences. In a previous study, *Ae. albopictus* was indicated to be more adaptable to wider temperature ranges than *Ae. aegypti* (Brady et al., 2013). This explains why *Ae. albopictus* can live in a wider geographical area in the north of China where temperatures vary greatly, whereas the habitat of *Ae. aegypti* is limited in perennial high temperature tropical areas. *Aedes albopictus* also shows greater adaptability to a larger range of precipitation, according to Bio 14 (Precipitation of driest month) and Bio 18 (Precipitation of warmest quarter). However, the relationship between precipitation and habitat suitability should be interpreted with caution. The lifecycle of *Aedes* mosquitoes is characterized by a process of dehydration of the eggs (several days to months) after spawning, and then rehydration to hatch once precipitation occurs (Tran et al., 2013; Leedale et al., 2016). Moreover, excessive rainfall can be detrimental to its development, through wash-out of eggs in water containers. This suggests that neither precipitation nor drought is the sufficient condition for the hatching of *Aedes* eggs. It is in fact the submergence of eggs caused by precipitation or artificial water storage at the appropriate time that triggers the hatching process. And previous studies reported different findings on the relationship between precipitation and the abundance of *Ae. aegypti* and *Ae. albopictus*, such as positive effects (Toma and Miyagi, 1990; Lourenço-de-Oliveira et al., 2004; Richards et al., 2006; Souza et al., 2010), negative effects (Roiz et al., 2010; Wee et al., 2013; Tokachil and Yusoff, 2018), or even no relationship (Luciano et al., 2003). Among the land-use types, croplands show a significant impact on the distribution of mosquitoes, either C3 crops or C4 crops. Agricultural irrigation can provide stable and abundant water for mosquito breeding. And human water supply is considered to have a greater impact on mosquito reproduction than natural precipitation (Roiz et al., 2010). Our model can only roughly reflect the adaptability of *Ae. aegypti* and *Ae. albopictus* to environmental variables. To understand the specific impact of the environment on mosquito survival and reproduction in Mainland China, further domestic ecological research is required.

According to our models, significant expansion of suitable habitat for both species can be observed. The area under mosquito threaten will increase to varying degrees under different climate scenarios (Fig. 7). Correspondingly, the exposed population will also increase (Fig. 8). Predictions under the RCP 8.5 scenario gives the worst outcome, followed by RCP 2.6 and RCP 4.5. This indicates that under the possible climate changes in the future twenty-first century, the living space of *Ae. aegypti* and *Ae. albopictus* in Mainland China will expand significantly, which will lead to increased populations burdened by a higher risk of infected with mosquito-borne diseases. Moreover, it should be noted that previous studies described the interspecific competition between these two species (Ho et al., 1989; Lounibos et al., 2002; Braks et al., 2004; Murrell and Juliano, 2008). This suggests that the co-existence of these two species could be investigated in the common habitat which predicted by our model.

Our study on the niche modeling of *Ae. aegypti* and *Ae. albopictus* in Mainland China does have some limitations. Firstly, there are relatively few occurrence records of *Ae. aegypti* so we could only use a small sample size. We therefore chose to use the Maxent model as it has shown advantage in terms of predictive performance for use with small sample sizes (Wisz et al., 2008). Among modeling algorithms that using presence-only records, Maxent is relatively insensitive to the sample size (which can be as small as 5) (Hernandez et al., 2006; van Proosdij et al., 2016). However, this limitation may still affect the accuracy of the model results. The small sample size is due to the fact that *Ae. aegypti* is currently only distributed in several southernmost provinces of Mainland China. Perhaps narrowing its modeling area would be a better approach. However, we believe that it was necessary to include *Ae. aegypti* into our model at the national level. *Aedes aegypti* plays a non-negligible role in the transmission of DF and its future invasive potential should be valued and assessed. Secondly, we have differentiated the population of urban and rural to estimate the exposed population. However, the possible change of urban extent within the study period was not considered. This may lead to a biased estimation of exposed population.

Our study is novel in our purpose on modeling not only the current distribution but also the future distribution of two important arbovirus vectors *Ae. aegypti* and *Ae. albopictus* in Mainland China. Based on the available datasets of predictions for future climate and land-use conditions, we established the model and estimated the extent and consequences (exposed area and population) of vector expansion. For the first time, an exhaustive understanding of the future status of *Ae. aegypti* and *Ae. albopictus* in Mainland China was carried out. Our findings can serve as a reference for current and future mosquito monitoring efforts and will contribute not only to the prevention and control of DF, but other mosquito-borne diseases as well.

According to ongoing global warming trends, continuous surveillance of *Ae. aegypti* and *Ae. albopictus* in the future is recommended in areas with higher habitat suitability predicted by our model. It will be helpful to investigate the spread of mosquitoes and to further validate the model. Moreover, further monitoring data can be used to improve and adjust the model. Based on our research, seasonal dynamic models can be further developed to provide more information on mosquito vectors.

5. Conclusion

Based on the high resolution environmental layers representing current and future climate and land-use conditions, we modeled the current and future distribution of arbovirus vector *Ae. aegypti* and *Ae. albopictus* in Mainland China. The current models performed well in representing the distribution of observed occurrence records. In the 2030s and 2050s models, both species were assumed to establish new habitats and expand their ecological niches as the climate changes. The change of area and population exposed to these two vectors in the future were also estimated under different climate scenarios. Our predictions have strategic implications for vector surveillance and the prevention of vector-borne diseases.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.01.301.

Acknowledgments

We would like to thank all researchers who contributed to this study by reporting collections of mosquitoes.

Funding: This work was supported by the National Project for Prevention and Control of Transboundary Animal Diseases (Grant No. 2017YFD0501800), the National Key R&D Program for the 13th Five-Year Plan, the Ministry of Science and Technology of the People's Republic

of China. This work was also supported by the National S&T programs of China (2015BAD12B05) and the Applied Technology Research and Development Plan of Heilongjiang, China (GA18B203). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

Arnould, J.P.Y., Monk, J., Ierodiaconou, D., Hindell, M.A., Semmens, J., Hoskins, A.J., et al., 2015. Use of anthropogenic sea floor structures by Australian fur seals: potential positive ecological impacts of marine industrial development? PLoS One 10, e0130581.

Baldwin, R.A., 2009. Use of maximum entropy modeling in wildlife research. Entropy 11, 854–866.

Benedict, M.Q., Levine, R.S., Hawley, W.A., Lounibos, L.P., 2007. Spread of the tiger: global risk of invasion by the mosquito *Aedes albopictus*. Vector Borne Zoonotic Dis. 7, 76–85.

Bhatt, S., Gething, P.W., Brady, O.J., Messina, J.P., Farlow, A.W., Moyes, C.L., et al., 2013. The global distribution and burden of dengue. Nature 496, 504–507.

Boes, K.E., Ribeiro, J.M., Wong, A., Harrington, L.C., Wolfner, M.F., Sirot, L.K., 2014. Identification and characterization of seminal fluid proteins in the Asian tiger mosquito, *Aedes albopictus*. PLoS Negl. Trop. Dis. 8, e2946.

Brady, O.J., Johansson, M.A., Guerra, C.A., Bhatt, S., Golding, N., Pigott, D.M., et al., 2013. Modelling adult *Aedes aegypti* and *Aedes albopictus* survival at different temperatures in laboratory and field settings. Parasit. Vectors 6, 351.

Braks, M.A.H., Honório, N.A., Lounibos, L.P., Lourençodeoliveira, R., Juliano, S.A., 2004. Interspecific competition between two invasive species of container mosquitoes, *Aedes aegypti* and *Aedes albopictus* (Diptera: *Culicidae*), in Brazil. Ann. Entomol. Soc. Am. 97, 130–139.

Brown, J.L., 2017. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol. Evol. 5, 694–700.

Brown, J.E., Evans, B.R., Zheng, W., Obas, V., Barreramartinez, L., Egizi, A., et al., 2014. Human impacts have shaped historical and recent evolution in *Aedes aegypti*, the dengue and yellow fever mosquito. Evolution 68, 514–525.

Chetan, N., Praveen, K.K., Vasudeva, G.K., 2014. Delineating ecological boundaries of Hanuman langur species complex in Peninsular India using MaxEnt modeling approach. PLoS One 9, e87804.

Chikerema, S.M., Murwira, A., Matope, G., Pfukenyi, D.M., 2013. Spatial modelling of *Bacillus anthracis* ecological niche in Zimbabwe. Prev. Vet. Med. 111, 25–30.

Conley, A.K., Fuller, D.O., Haddad, N., Hassan, A.N., Gad, A.M., Beier, J.C., 2014. Modeling the distribution of the West Nile and Rift Valley fever vector *Culex pipiens* in arid and semi-arid regions of the Middle East and North Africa. Parasit. Vectors 7, 289.

Cunze, S., Koch, L.K., Kochmann, J., Klimpel, S., 2016. *Aedes albopictus* and *Aedes japonicus* - two invasive mosquito species with different temperature niches in Europe. Parasit. Vectors 9, 573.

Dan, L.W., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21, 335–342.

Elith, J., Graham, C., Anderson, R., Dudik, M., Ferrier, S., Guisan, A., et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342.

Escobar, L.E., Qiao, H., Cabello, J., Peterson, A.T., 2018. Ecological niche modeling re-examined: a case study with the Darwin's fox. Ecol. Evol. 8, 4757–4770.

Fan, J., Ma, T., Zhou, C., Zhou, Y., Xu, T., 2014. Comparative estimation of urban development in China's cities using socioeconomic and DMSP/OLS night light data. Remote Sens. 6, 7840–7856.

Ferreira, G.L., 2012. Global dengue epidemiology trends. Rev. Inst. Med. Trop. Sao Paulo 54, S5.

Gao, X., Wang, H., Wang, H., Qin, H., Xiao, J., 2016. Land use and soil contamination with *Toxoplasma gondii* oocysts in urban areas. Sci. Total Environ. 568, 1086–1091.

Gao, X., Xiao, J.H., Liu, B.Y., Wang, H.B., 2018. Impact of meteorological and geographical factors on the distribution of *Phlebotomus chinensis* in northwestern mainland China. Med. Vet. Entomol. 32, 365–371.

Gubler, D.J., 2012. Dengue, urbanization and globalization: the unholy trinity of the 21st century. Int. J. Infect. Dis. 16, 3–11.

Hales, S., De, W.N., Maindonald, J., Woodward, A., 2002. Potential effect of population and climate changes on global distribution of dengue fever: an empirical model. Lancet 360, 830.

Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29, 773–785.

Ho, B.C., Ewert, A., Chew, L.M., 1989. Interspecific competition among *Aedes aegypti*, *Ae. albopictus*, and *Ae. triseriatus* (Diptera: *Culicidae*): larval development in mixed cultures. J. Med. Entomol. 26, 615–623.

Jentes, E.S., Poumerol, G., Gershman, M.D., Hill, D.R., Lemarchand, J., Lewis, R.F., et al., 2011. The revised global yellow fever risk map and recommendations for vaccination, 2010: consensus of the Informal WHO Working Group on Geographic Risk for Yellow Fever. Lancet Infect. Dis. 11, 622–632.

Jianren, H., 1991. The eradication of *Aedes aegypti* applying biocontrol measures in Guangxi, PRC. Chin. J. Vector Biol. Control 4, 005.

Joubert, D.A., O'Neill, S.L., 2017. Comparison of stable and transient Wolbachia infection models in *Aedes aegypti* to block dengue and West Nile viruses. PLoS Negl. Trop. Dis. 11, e0005275.

Kong, L., Wang, J., Li, Z., Lai, S., Liu, Q., Wu, H., et al., 2018. Modeling the heterogeneity of dengue transmission in a city. Int. J. Environ. Res. Public Health 15, 1128.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., et al., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Divers. Distrib. 19, 1366–1379.

Kubota, Y., Shiono, T., Kusumoto, B., 2015. Role of climate and geohistorical factors in driving plant richness patterns and endemicity on the east Asian continental islands. Ecography 38, 639–648.

Leedale, J., Jones, A.E., Caminade, C., Morse, A.P., 2016. A dynamic, climate-driven model of Rift Valley fever. Geospat. Health 11, 394.

Leparc-Goffart, I., Nougairede, A., Cassadou, S., Prat, C., De, L.X., 2014. Chikungunya in the Americas. Lancet 383, 514.

Li, H.X., Zhou, H.N., Yang, Y.C., Jiang, H., 2010. Dengue fever epidemic situation in Yunnan province from 2004 to 2008. Chin. J. Vector Biol. Control 21, 576–577,580.

Liu, C., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. J. Biogeogr. 40, 778–789.

Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2010. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.

Lounibos, L.P., Suárez, S., Menéndez, Z., Nishimura, N., Escher, R.L., O'Connell, S.M., et al., 2002. Does temperature affect the outcome of larval competition between *Aedes aegypti* and *Aedes albopictus*? J. Vector Ecol. 27, 86.

Lourenço-de-Oliveira, R., Castro, M.G., Braks, M.A., Lounibos, L.P., 2004. The invasion of urban forest by dengue vectors in Rio de Janeiro. J. Vector Ecol. 29, 94–100.

Luciano, T., Severini, I.F., Di Luca, I.M., Bella, I.A., Roberto, R., 2003. Seasonal patterns of oviposition and egg hatching rate of *Aedes albopictus* in Rome. J. Am. Mosq. Control Assoc. 19, 100.

Ma, T., Zhou, C., Pei, T., Haynie, S., Fan, J., 2012. Quantitative estimation of urbanization dynamics using time series of DMSP/OLS nighttime light data: a comparative case study from China's cities. Remote Sens. Environ. 124, 99–107.

Manyangadze, T., Chimbari, M.J., Gebreslasie, M., Ceccato, P., Mukaratirwa, S., 2016. Modelling the spatial and seasonal distribution of suitable habitats of schistosomiasis intermediate host snails using Maxent in Ndumo area, KwaZulu-Natal Province, South Africa. Parasit. Vectors 9, 572.

Miller, R.H., Masuoka, P., Klein, T.A., Kim, H.C., Somer, T., Grieco, J., 2012. Ecological niche modeling to estimate the distribution of Japanese encephalitis virus in Asia. PLoS Negl. Trop. Dis. 6 (6(2012-6-19)), 119–121 6.

Morrison, A.C., Zielinskigutierrez, E., Scott, T.W., Rosenberg, R., 2008. Defining challenges and proposing solutions for control of the virus vector *Aedes aegypti*. PLoS Med. 5, e68.

Moutailler, S., Krida, G., Schaffner, F., Vazeille, M., Failloux, A.B., 2008. Potential vectors of Rift Valley fever virus in the Mediterranean region. Vector Borne Zoonotic Dis. 8, 749.

Murray, N.E., Quam, M.B., Wildersmith, A., 2013. Epidemiology of dengue: past, present and future prospects. Clin. Epidemiol. 2013, 299–309.

Murrell, E.G., Juliano, S.A., 2008. Detritus type alters the outcome of interspecific competition between *Aedes aegypti* and *Aedes albopictus* (Diptera: *Culicidae*). J. Med. Entomol. 45, 375–383.

Olivero, J., Toxopeus, A.G., Skidmore, A.K., Real, R., 2016. Testing the efficacy of downscaling in species distribution modelling: a comparison between MaxEnt and favourability function models. Anim. Biodivers. Conserv. 39, 99–114.

Ooi, E.-E., Goh, K.-T., Gubler, D.J., 2006. Dengue prevention and 35 years of vector control in Singapore. Emerg. Infect. Dis. 12, 887.

Peterson, A.T., Papeş, M., Soberón, J., 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol. Model. 213, 63–72.

Phillips, S.J., 2017. A Brief Tutorial on Maxent. http://biodiversityinformatics.amnh.org/open_source/maxent/Maxent_tutorial2017.pdf.

Phillips, S.J., Dudík, M., 2010. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., et al., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197.

Pradhan, P., 2016. Strengthening MaxEnt modelling through screening of redundant explanatory bioclimatic variables with variance inflation factor analysis. Researcher 8, 29–34.

Ren, Z., Wang, D., Ma, A., Hwang, J., Bennett, A., Sturrock, H.J.W., et al., 2016. Predicting malaria vector distribution under climate change scenarios in China: challenges for malaria elimination. Sci. Rep. 6, 20604.

Richards, S.L., Apperson, C.S., Ghosh, S.K., Cheshire, H.M., Zeichner, B.C., 2006. Spatial analysis of *Aedes albopictus* (Diptera: *Culicidae*) oviposition in suburban neighborhoods of a Piedmont community in North Carolina. J. Med. Entomol. 43, 976–989.

Roiz, D., Rosa, R., Arnoldi, D., Rizzoli, A., 2010. Effects of temperature and rainfall on the activity and dynamics of host-seeking *Aedes albopictus* females in northern Italy. Vector Borne Zoonotic Dis. 10, 811–816.

Sallam, M.F., Xue, R.-D., Pereira, R.M., Koehler, P.G., 2016. Ecological niche modeling of mosquito vectors of West Nile virus in St. John's County, Florida, USA. Parasit. Vectors 9, 371.

Small, C., Pozzi, F., Elvidge, C.D., 2005. Spatial analysis of global urban extent from DMSP-OLS night lights. Remote Sens. Environ. 96, 277–291.

Souza, S.S.D., Silva, I.G.D., Silva, H.H.G.D., 2010. Association between dengue incidence, rainfall and larval density of *Aedes aegypti*, in the state of Goiás. Rev. Soc. Bras. Med. Trop. 43, 152.

Sutton, P.C., 2003. A scale-adjusted measure of "urban sprawl" using nighttime satellite imagery. Remote Sens. Environ. 86, 353–369.

Tan, Y., Feng, X., Jiang, J., 2004. Analysis on the dengue vector surveillance results during 2002–2003 in Guangxi. Chin. J. Hyg. Insecticides Equip. 10, 154–156.

Tokachil, N., Yusoff, N., 2018. Effect of rainfall duration on *Aedes aegypti* population. AIP Conference Proceedings. 1974. AIP Publishing, p. 020081.

Toma, T., Miyagi, I., 1990. Seasonal changes in the hatchability of *Aedes albopictus* (Diptera: *Culicidae*) eggs in Okinawajima, Ryukyu archipelago, Japan. Med. Entomol. Zool. 41, 195–204.

Tran, A., L'Ambert, G., Lacour, G., Benoît, R., Demarchi, M., Cros, M., et al., 2013. A rainfall- and temperature-driven abundance model for *Aedes albopictus* populations. Int. J. Environ. Res. Public Health 10, 1698–1719.

van Proosdij, A.S.J., Sosef, M.S.M., Wieringa, J.J., Raes, N., 2016. Minimum required number of specimen records to develop accurate species distribution models. Ecography 39, 542–552.

Vuuren, D.P.V., Stehfest, E., Elzen, M.G.J.D., Kram, T., Vliet, J.V., Deetman, S., et al., 2011. RCP2.6: exploring the possibility to keep global mean temperature increase below 2 °C. Clim. Chang. 109, 95.

Wang, L., Hu, W., Soares Magalhaes, R.J., Bi, P., Ding, F., Sun, H., et al., 2014. The role of environmental factors in the spatial distribution of Japanese encephalitis in mainland China. Environ. Int. 73, 1–9.

Wee, L.K., Weng, S.N., Raduan, N., Wah, S.K., Ming, W.H., Shi, C.H., et al., 2013. Relationship between rainfall and *Aedes* larval population at two insular sites in Pulau Ketam, Selangor, Malaysia. Southeast Asian J. Trop. Med. Public Health 44, 157–166.

Wildersmith, A., Engeong, O., Vasudevan, S.G., Gubler, D.J., 2010. Update on dengue: epidemiology, virus evolution, antiviral drugs, and vaccine development. Curr. Infect. Dis. Rep. 12, 157–164.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. 14, 763–773.

Wu, J.Y., Lun, Z.R., James, A.A., Chen, X.G., 2010. Dengue fever in Mainland China. Am. J. Trop. Med. Hyg. 83, 664.

Xu, G., Dong, H., Shi, N., Liu, S., Zhou, A., Cheng, Z., et al., 2007. An outbreak of dengue virus serotype 1 infection in Cixi, Ningbo, People's Republic of China, 2004, associated with a traveler from Thailand and high density of *Aedes albopictus*. Am. J. Trop. Med. Hyg. 76, 1182–1188.

Yong, H.X., Xia, M.H., Feng, W.H., Hua, D.Y., Jia, S., Le, L.X., et al., 2014. Outbreak of dengue fever in central China, 2013. Biomed. Environ. Sci. 27, 894–897.

Zhang, H., Zhang, Y., Hamoudi, R., Yan, G., Chen, X., Zhou, Y., 2014. Spatiotemporal characterizations of dengue virus in mainland China: insights into the whole genome from 1978 to 2011. PLoS One 9, e87630.

Zhang, K., Yao, L., Meng, J., Tao, J., 2018. Maxent modeling for predicting the potential geographical distribution of two peony species under climate change. Sci. Total Environ. 634, 1326.